
Phenotypic modifications to conspecific density arising from predation risk assessment

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Organisms often perceive predation risk through visual, auditory, or chemical cues that accompany or persist after an attack on *other* prey individuals. In this paper an argument is developed that suggests that it is adaptive for species that use such indirect cues to include conspecific density in the assessment of predation risk, and to respond to conspecific density by modifying phenotype (e.g. behavior, morphology of life history). A model based on this argument predicts that at equivalent (including negligible) indirect cue levels an organism should adopt less vulnerable phenotypes at lower conspecific density. Further, the phenotypic modifications to differences in conspecific density are predicted to be on the same order of magnitude as phenotypic responses to differences in predator density, to be more pronounced at higher indirect cue levels, and can be extended to responses to differences in the density of heterospecific species that share predators. This “risk assessment” mechanism is qualitatively different from other mechanisms, such as the dilution and “many eyes” effects that predict behavioral responses to conspecific density. If species use conspecific or heterospecific density to assess predation risk as predicted, there may be implications for the role and evolution of traits used to perceive conspecific and heterospecific densities, species aggregation, and population dynamics, and should be considered in the design of experiments of nonlethal effects of predators.

It is increasingly recognized that species respond to predation risk by modifying phenotype (reviewed in Lima and Dill 1990, Chivers and Smith 1998, Kats and Dill 1998, Lima 1998, Tollrian and Harvell 1999). This facility presents clear benefits to the survival of an organism and its offspring in habitats in which predation risk is spatially and temporally variable (Gilliam 1982, Abrams 1987, Stearns 1989, West-Eberhard 1989, Houston et al. 1993, Werner and Anholt 1993, Agrawal 2001), because more vulnerable phenotypes allow faster resource acquisition, whereas less vulnerable phenotypes reduce predation risk. To react adaptively to predator presence and absence, prey must be able to

accurately assess predation risk; they must minimally be able to recognize predator presence and optimally gauge the density of predators and the threat they represent.

Many species assess predation risk, in part or in whole, with indirect cues of successful or unsuccessful attacks on conspecific or heterospecific organisms, rather than by direct detection of predators, including through escaped attacks (hereafter direct detection). Indirect cues (*sensu* Dicke and Grostal 2001) arise during or after attack events, and are perceived in various ways through visual, chemical, or auditory cues of attack events, injured conspecifics, or cues in feces or other exudates of predator digestion of prey (reviewed in Lima and Dill 1990, Chivers and Smith 1998, Kats and Dill 1998, Lima 1998, Tollrian and Harvell 1999). Even when prey may appear to directly detect a predator, past predation events and hence indirect cues, as defined here, may be important. For example, many species that react to predators through chemical cues react more strongly or, in some cases, only to predators that have fed on conspecifics or heterospecifics from the same habitat (Wilson and Lefcort 1993, Chivers et al. 1996, Laurila et al. 1998, Levri 1998, Yamada et al. 1998, Jacobson and Stabell 1999, Madison et al. 1999, Murray and Jenkins 1999, Chivers and Mirzal 2001, Persons et al. 2001, reviewed in Chivers and Smith 1998, Kats and Dill 1998). Further, many studies have demonstrated that species react to indirect cues of simulated predation events (i.e. to injured, disturbed, or killed conspecifics) in the absence of any possible direct predator assessment (Levri 1998, Jacobson and Stabell 1999, Kiesecker et al. 1999, Belden et al. 2000, Hazlett and McLay 2000, Bouwma and Hazlett 2001, Bryer et al. 2001, reviewed in Chivers and Smith 1998, Kats and

Dill 1998). For example, Turner (1997) showed that pulmonate snails (*Physella gyrina*) respond to crushed conspecifics (in the absence of predators) by modifying behavior to avoid predation risk. Although ecologists do not typically evaluate predator cues in terms of whether they originate from direct detection or indirect cues of predator presence, there is much evidence that indirect cues are used in part or in whole by many species (Dicke and Grostal 2001).

I hypothesize in this paper that to respond adaptively to predation risk signaled by indirect cues, organisms should modify phenotype as a function of conspecific density in addition to the cue level. Because the indirect cue level is a function of both predator and conspecific density, an organism can only accurately determine the level of predation risk if it assesses cue level in conjunction with estimates of conspecific density. For example, if an organism perceives indirect cues that indicate one conspecific is killed per day, this will indicate much higher predation risk to an individual in a community with 20, rather than 2000, conspecific individuals. Therefore, at lower conspecific density, a perceived indirect cue represents a higher predation risk, and it is adaptive to employ a less vulnerable phenotype. Hereafter the less vulnerable phenotypes employed by animals at high predation risk are denoted as higher-risk phenotypes. Conversely, the more vulnerable phenotypes employed at low predation risk are denoted as lower-risk phenotypes.

The argument

I constructed a model to examine adaptive prey responses to changes in indirect predator cue level and conspecific density. Whereas I focus on responses to conspecific individuals, predictions of the model can be extended to heterospecific prey of the predator. I assume a constant background predation risk level, and therefore do not address responses to localized individual predation events in which predation risk would exhibit strong peaks in time as a result of encounters. The model applies to prey that gauge predation risk through indirect cues, as defined in the Introduction, that result from failed or successful predation events involving conspecific prey individuals. For simplicity, I assume that predation rate is linearly proportional to prey density and predator density (i.e. I use the Holling's Type I functional response). Using a nonlinear response will not affect the general qualitative predictions made here.

The model compares the actual and perceived predation risk of an individual forager as a function of its ability to use conspecific density in predation risk assessment. The actual predation risk to a single prey individual, r_{act} , is defined as the per capita prey capture

rate of an individual predator, a , times predator density, P ,

$$r_{act} = aP \quad (1)$$

That is, the risk is the rate at which individual prey are captured, which is equivalent to the total predation rate divided by prey density. The magnitude of the indirect cue generated by predation, Q , is proportional to the rate prey are captured

$$Q = \rho CaP \quad (2)$$

C is prey density, and ρ is a constant that converts the number of predation events to the indirect cue level. If prey use conspecific density in predation risk assessment, then we can express the perceived predation risk as

$$r_{per} = f(C)Q = f(C)\rho CaP \quad (3)$$

where $f(C)$ transforms the indirect cue level to perceived predation risk given conspecific density.

Consider first the perceived predation risk of a prey that cannot incorporate prey density into assessment of predation risk, but relies solely on the indirect cue level. Then $f(C)$ is a constant, and (using the above equations) the perceived predation risk is proportional to the cue

$$r_{per} \sim Q = \rho Cr_{act} \quad (4)$$

Assessing predation risk in the absence of information of conspecific density can thus yield a very poor assessment of predation risk (Fig. 1). Predation risk is underestimated at low prey density and overestimated at high prey density (Fig. 1). Indeed, it appears that modifying phenotype in response to indirect predation cue level could have little adaptive value if there were no assessment of conspecific density.

Next consider the case in which prey can accurately assess conspecific density and respond adaptively to both predator cue levels and conspecific density levels. In this case, the perceived risk is equal to the actual risk, and therefore

$$f(C) = \frac{aP}{\rho aCP} = \frac{1}{\rho C} \quad (5)$$

which means

$$r_{per} = \frac{Q}{\rho C} = r_{act} \quad (6)$$

That is, given equal predator cue levels, perceived predation risk is inversely proportional to prey density. If prey can incorporate conspecific density into preda-

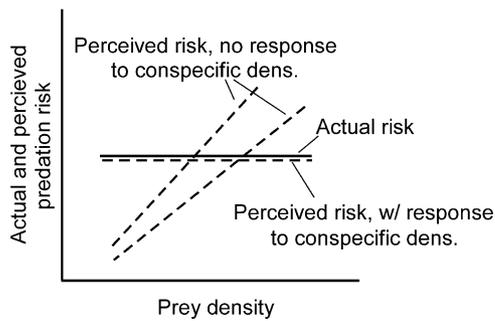


Fig. 1. Perceived risk (dashed lines) and actual risk (solid line) as a function of prey density at constant predator density. A Holling's type I functional response is assumed, and the actual risk is assumed to be proportional to the consumption rate of prey (see text). If prey are unable to incorporate prey density into risk assessment, then perceived risk will be proportional to the cue level, which is proportional to prey density. In this case, the perceived risk will underestimate or overestimate the actual risk at low and high prey density, respectively, as illustrated by two potential examples (different ρ in eq. (4)). If prey are able to assess and incorporate prey density into risk assessment adaptively, then the perceived risk will equal the actual risk at all prey densities.

tion risk assessment as expressed in eq. (6), then even at very different indirect cue levels that occur at low and high prey density and the same predator density, the organism can perceive the same (correct) predation risk (Fig. 1).

The model can be used to derive specific testable predictions. For example, at equal indirect predation cue level, prey are predicted to adopt lower-risk phenotypes at higher conspecific densities (eq. (6)). Further, at higher conspecific densities, an increase in (absolute) cue level will represent a smaller increase in perceived risk (eq. (6)) and therefore elicit a less-pronounced phenotypic response. This prediction is intuitive; a given increase in absolute cue level suggests a larger predator density increase if there are few conspecifics than if there are many conspecifics.

The risk-assessment mechanism can likely be extended to some systems in which predation cue is absent. In natural systems, predation risk may vary over time and space, but may hypothetically never be zero even if the predation cue level is not perceptible (Lima and Dill 1990). This is because predation events occur even after finite periods of time of zero predation events. Therefore, the model predictions can be extended to the limit of predator absence, and an organism is predicted to adopt a higher risk phenotype at lower conspecific densities even in the absence of predation cue. In contrast, for systems in which prey density is high, and indirect cues diffuse quickly and uniformly, such as for zooplankton-predator systems, the absence of any predation cue is likely a strong sign that predation risk is absent. Therefore, if there is no indirect cue in such systems, the risk-assessment mechanism is not likely to be important.

Discussion

The argument developed here creates a framework for what is otherwise an intuitive concept: If an organism gauges predation risk by indirect cues, then it must accurately assess and respond to both cue level and *conspecific density* in order to select an adaptive phenotype. This is intuitive because it is basic to the way that we gauge risk. For example, the knowledge that 10 people are assaulted per month in a particular city does not fully determine if the city is relatively dangerous. Not unless we factor in the city's population size could we properly modify our behavior for safety considerations. Similarly, an organism's assessment of predation risk based on indirect cue level but not on conspecific density will likely underestimate or overestimate actual risk (Fig. 1). As reviewed in the Introduction, there is much evidence that both terrestrial and aquatic organisms use indirect cues to evaluate predation risk, demonstrating an important component of the risk-assessment mechanism. Given the importance of responding adaptively to predation risk (Abrams 1987, Werner and Anholt 1993, reviewed in Lima and Dill 1990, Chivers and Smith 1998, Kats and Dill 1998, Lima 1998, Schmitz 1998, Tollrian and Harvell 1999), and the demonstrated ability of organisms to perceive the presence of individuals from their own and other species (Lima 1990, Hokit and Blaustein 1994, Beauchamp 1998, Ojanguren and Brana 1999, Childress and Herunkind 2000), it is plausible that phenotypic responses to conspecific density due to the mechanisms suggested here could be a general response of many species.

Perhaps surprising is the large magnitude of the predicted effect of conspecific density on phenotype; a reduction in conspecific density at an equal indirect cue level is predicted to have the same effect as an equivalent increase in predator density (eq. (5) and (6)). Of course, in a natural setting changes in conspecific and predator density will affect the indirect cue level, and therefore controlled experiments may be required to examine the relative magnitudes of responses to conspecific density. Whereas this equivalence is dependent on the Type I functional response assumption used in the model, the prediction of the nearly equivalent magnitudes of the responses to conspecific and predator density is striking. Further, theory predicts that changes in resource density will have a weaker or equivalent affect than equivalent changes in predator density (Werner and Anholt 1993). This suggests that changes in competitor density could elicit changes on the same order of magnitude as changes in resource density. Note that although I have evaluated the phenotypic response to predator cues in the absence of other prey species, indirect cues of a predator preying on heterospecific species that share a predator could be modeled with a similar framework as that presented here.

The prediction that a species will display higher risk behavior at higher conspecific density is also predicted to be a potential consequence of the “many eyes effect” and “dilution effect” (Pulliam 1973, Bertram 1978, Dehn 1990, McNamara and Houston 1992, reviewed in Elgar 1989, Lima 1990, Roberts 1996). In the many eyes effect, an individual organism’s ability to detect predator risk is increased through warning signals or behavioral reactions of other potential prey (conspecific or heterospecific) that have detected predator presence. In the dilution effect, the probability of capture by a predator is predicted to decrease as group size increases, as other individuals may be captured and thus risk is “diluted”. These effects are typically discussed in the context of species that show grouping behavior, but can hypothetically be extended to species that do not show grouping behavior. In both cases, there is no definitive prediction that higher risk phenotype will be adopted as group size increases and thereby keep predation risk constant and lower the costs of utilizing higher risk phenotypes (Roberts 1996). Rather, prey may also utilize the same phenotype, but enjoy less predation risk in larger groups.

Given the similar predictions of the risk assessment mechanism proposed here, and the dilution and many eyes mechanisms, it may be difficult to determine which mechanisms are operating. For example, if, at equal indirect cue levels, an organism displays a higher risk phenotype at increased densities, is this because the higher density indicates there is less actual predation threat, or because a higher density actually reduces the predation threat? Comparison of experimental results with quantitative predictions of the different effects may be necessary in order to distinguish between different mechanisms. If, for example, a large phenotypic response accompanies an increase in conspecific density at a constant cue level for a species in which the dilution effect and many eyes effect can be predicted to be low, then the risk assessment effect is a probable mechanism. Further, examination of particular phenotypic responses may help to determine the relative significance of the different mechanisms. For example, at equal indirect cue levels (e.g. through experimental manipulation), a reduction in predator-induced morphological defenses at higher conspecific density is predicted by the risk-assessment mechanism, but unlikely result from the dilution or many-eyes effects.

Results of a number of empirical studies are suggestive of the risk assessment mechanism. Golden et al. (2001) examined the behavior of northern leopard frog (*Rana pipiens*) tadpoles in isolation and in the presence of conspecifics in 19 l aquaria. They found that in the presence of five conspecifics, tadpoles displayed more pronounced higher-risk behavior than when alone. For example, tadpoles were on average more than 3 times as likely to swim at the higher density. Relyea (2002) reports a similar effect of density on wood frog (*Rana*

sylvatica) behavior, in which a doubling of wood frog density caused a 50% increase in tadpole activity. Further, in a mesocosm experiment, I found that wood frog tadpole growth at increased tadpole density was much less affected by equal indirect cues of caged larval dragonflies (Peacor, unpubl.). The risk assessment mechanism is a good candidate for these patterns as other mechanisms are unlikely; the studied tadpoles forage relatively independently, and therefore likely do not benefit from the dilution effect or the many eyes effect. Further, in all of these studies, the resource level reduction that may accompany increased prey density was not responsible for the observed changes in prey behavior (e.g. as in Grand and Dill 1999). A study by Tollrian (Am. Soc. Limnol. Oceanogr. 2002 summer meeting abstracts) showed morphological responses that are also suggestive of the risk-assessment mechanism; in the presence of chemical predator cues, induction of morphological defenses in cladocerans, rotifers and ciliates was less pronounced at higher conspecific densities.

The risk assessment mechanism proposed here has implications for species aggregation. In a natural system a predator will capture prey at irregular intervals, and therefore indirect cues from individual predators can occur intermittently. The variability of the total cue from all predators will be a function of predation event frequency and the duration of the predation cue. For example, chemical cues of predation events in aquatic systems can remain in water for days. The duration is a function of the density of microorganisms which negate the cue (Loose et al. 1993, Peacor, unpubl.) and is also likely dependent on other environmental factors such as water circulation. Of course, some forms of indirect cues will be immediate and of short duration, as in the case of visual indirect cues of predators attacking other prey. The cue variability for a system in which individual predation events occur randomly, and for which the cue magnitude decreases exponentially over time, is shown as a function of prey density and cue duration in Fig. 2. As expected, the variability of the indirect cue decreases as a function of the density of predation events and of cue duration. As prey density increases, the indirect cue level becomes less variable and, consequently, a more reliable measure of predation risk. Higher conspecific density may have a positive effect on fitness because the consequent increase in accuracy of predation risk assessment facilitates the adoption of an adaptive phenotype in a variable environment. Thus predation risk assessment could contribute to the evolution of species aggregation and of traits that facilitate the evaluation of conspecific density. For example, the risk-assessment mechanism could explain the counterintuitive finding of several researchers that, in some conditions, mosquitoes prefer to lay eggs in water that contains a higher density of eggs (Heard 1994, Edgerly et al. 1998). Whereas one might expect that mosquitoes

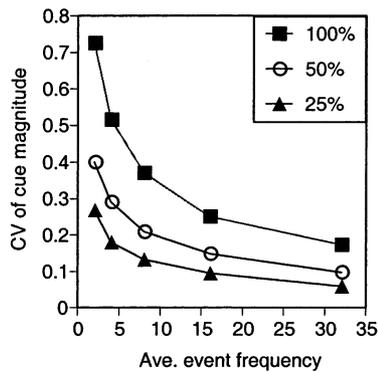


Fig. 2. Variation in cue level, expressed as the coefficient of variation ($CV = \text{stdev}/\text{average}$), as a function of predation event frequency and duration of cue signal. The number of predation events per time interval was selected from a Poisson distribution, with the average value plotted on the x axis. The cue signal of each event degraded by 25%, 50%, or 100% per time interval. Increasing frequency of events (that would accompany higher prey or predator density) and cue duration both cause a decrease in the variation in the overall cue level.

should avoid laying eggs where egg density is already high, the resultant higher larval densities can also have a positive effect by allowing a better assessment of predation risk (Fig. 2).

Long-term population dynamics of a species could be affected by the predictions made here concerning adaptive modifications of phenotype in response to conspecific density. Whereas most population and community level models that include phenotypic responses to predators are based on the assumption that species have perfect knowledge of predation risk, a recent theoretical study of Luttbegg and Schmitz (2000) indicates that accuracy of predation risk evaluation can strongly affect long-term dynamics. Luttbegg and Schmitz therefore call for increased attention to the manner and ability of species to assess predation risk. In their model, Luttbegg and Schmitz assume that predation risk assessment is proportional to the number of encounters between an organism and predators. However, if the species uses indirect cues, then predation risk evaluation will depend on conspecific density and cue duration (Fig. 2). Thus, the accuracy of predation risk evaluation can be very different even at the same predator density, and could actually be very high at low predator but high conspecific density. Therefore, to determine the ability of prey to evaluate predation risk and hence model the influence of phenotypic responses to predation risk on long-term dynamics, it is instructive to consider the degree to which prey can assess direct encounters and indirect cues to estimate predation risk.

The direct and indirect effects of phenotypic responses to predator risk on the responding species, and on species with which the responding species interacts (i.e. its resources or other predators), are receiving

increasing attention from ecologists (Turner and Mittelbach 1990, Huang and Sih 1991, McIntosh and Townsend 1996, Beckerman et al. 1997, Peacor and Werner 1997, Turner 1997, Peckarsky and McIntosh 1998, Relyea 2000, Abrams et al. 1996, reviewed in Werner and Peacor 2003, and Bolker et al. 2003). Strong arguments have been presented that such effects, denoted trait-mediated effects or nonlethal predator effects, can contribute substantially to net predator effects. If the risk assessment effect proposed here is operative, this could have implications for the design of experiments on nonlethal predator effects. To study nonlethal predator effects, ecologists often use indirect cues of predation to isolate the nonlethal predator effects from lethal effects. But, if study organisms evaluate conspecific or heterospecific prey density in the assessment of predation risk, then the perceived predation risk will be different in different conspecific and heterospecific density treatments. This could confound comparison across experiments of the magnitude of nonlethal predator effects on phenotype and fitness responses such as growth and survival, and confound applications of laboratory results to predictions in natural settings. Future experiments of nonlethal predator effects could benefit from considering this potentially confounding factor.

Conclusions

The argument and model developed here suggests that when an organism uses indirect cues to sense predation risk, in large part or in whole, it is necessary for the organism to assess and respond to the density of conspecifics (or heterospecifics that share predators) in order to adopt an adaptive phenotype. The conspecific or heterospecific species' densities do not directly affect fitness, but rather serve as an *indicator* of an environmental condition (in this case predation risk) that does affect fitness. Several empirical studies are consistent with model predictions, although none have been designed to determine the significance of the risk-assessment mechanism relative to alternative mechanisms. Use of conspecific or heterospecific density by species to assess predation risk, as predicted by the model, could have implications for the evolution of perception of conspecific and heterospecific densities, species aggregation, and population dynamics, and should be considered in the design of experiments of nonlethal effects of predators.

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References

- Abrams, P. A. 1987. Indirect interactions between species that share a predator: varieties on a theme. – In: Kerfoot, W. C. and Sih, A. (eds), *Predation: direct and indirect impacts on aquatic communities*. Univ. Press of New England, pp. 38–54.
- Abrams, P. A., Menge, B. A., Mittelbach, G. G. et al. 1996. The role of indirect effects in food webs. – In: Polis, G. A. and Winemiller, K. O. (eds), *Food webs: integration of patterns and dynamics*. Chapman and Hall, pp. 371–395.
- Agrawal, A. A. 2001. Phenotypic plasticity in the interactions and evolution of species. – *Science* 294: 321–326.
- Beauchamp, G. 1998. The effect of group size on mean food intake rate in birds. – *Biol. Rev. Cambridge Philos. Soc.* 73: 449–472.
- Beckerman, A. P., Uriarte, M. and Schmitz, O. J. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. – *Proc. Nat. Acad. Sci. USA* 94: 10735–10738.
- Belden, L. K., Wildly, E. L., Hatch, A. C. and Blaustein, A.R. 2000. Juvenile western toads, *Bufo boreas*, avoid chemical cues of snakes fed juvenile, but not larval, conspecifics. – *Anim. Behav.* 59: 871–875.
- Bertram, B. C. R. 1978. Living in groups: predators and prey. – In: Krebs, J. R. and Davies, N. B. (eds), *Behavioural ecology: An evolutionary approach*. Blackwell Scientific Publications, pp. 64–96.
- Bolker, B., M. Holyoak, V. Krivan, L. et al. 2003. Connecting theoretical and empirical studies of trait-mediated interactions. – *Ecology*, in press.
- Bouwma, P. and Hazlett, B. A. 2001. Integration of multiple predator cues by the crayfish *Orconectes propinquus*. – *Anim. Behav.* 61: 771–776.
- Bryer, P. J., Mirza, R. S. and Chivers, D. P. 2001. Chemosensory assessment of predation risk by slimy sculpins (*Cottus cognatus*): responses to alarm, disturbance, and predator cues. – *J. Chem. Ecol.* 27: 533–546.
- Childress, M. J. and Herrnkind, W. F. 2000. The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. – *Anim. Behav.* 62: 465–472.
- Chivers, D. P. and Smith, R. J. F. 1998. Chemical alarm signaling in aquatic predator-prey systems: A review and prospectus. – *Ecoscience* 5: 338–352.
- Chivers, D. P. and Mirzal, R. S. 2001. Importance of predator diet cues in responses of larval wood frogs to fish and invertebrate predators. – *J. Chem. Ecol.* 27: 45–51.
- Chivers, D. P., Wisenden, B. D. and Smith, R. J. F. 1996. Damsel larvae learn to recognize predators from chemical cues in the predator's diet. – *Anim. Behav.* 52: 315–320.
- Dehn, M. M. 1990. Vigilance for predators: detection and dilution effects. – *Behav. Ecol. Sociobiol.* 26: 337–342.
- Dicke, M. and Grostal, P. 2001. Chemical detection of natural enemies by arthropods: an ecological perspective. – *Annu. Rev. Ecol. Syst.* 32: 1–23.
- Eggerly, J. S., McFarland, M., Morgan, P. and Livdahl, T. 1998. A seasonal shift in egg-laying behavior in response to cues of future competition in a treehole mosquito. – *J. Anim. Ecol.* 67: 805–818.
- Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. – *Biol. Rev. Cambridge Philos. Soc.* 64: 13–33.
- Gilliam, J. F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. PhD Thesis, Michigan State Univ.
- Golden, D. R., Smith, G. R. and Rettig, J. E. 2001. Effects of age and group size on habitat selection and activity level in *Rana pipiens* tadpoles. – *Herpetol. J.* 11: 69–73.
- Grand, T. C. and Dill, L. M. 1999. The effect of group size on the foraging behaviour of juvenile coho salmon: reduction of predation risk or increased competition? – *Anim. Behav.* 58: 443–451.
- Hazlett, B. A. and McLay, C. 2000. Contingencies in the behaviour of the crab *Heterozius rotundifrons*. – *Anim. Behav.* 59: 965–974.
- Heard, S. B. 1994. Imperfect oviposition decisions by the picture plant mosquito (*Wyeomyia smithii*). – *Evol. Ecol.* 8: 493–502.
- Hokit, D. G. and Blaustein, A. R. 1994. The effects of kinship on growth and development in tadpoles of *Rana cascadae*. – *Evolution* 48: 1383–1388.
- Houston, A. I., McNamara, J. M. and Hutchinson, J. M. C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. – *Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci.* 341: 375–397.
- Huang, C. F. and Sih, A. 1991. Experimental studies on direct and indirect interactions in a 3 trophic-level stream system. – *Oecologia* 85: 530–536.
- Jacobson, H. P. and Stabell, O. B. 1999. Predator-induced alarm responses in the common periwinkle, *Littorina littorea*: dependence on season, light condition, and chemical labeling of predators. – *Marine Biol.* 134: 551–557.
- Kats, L. B. and Dill, L. M. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. – *Ecoscience* 5: 361–394.
- Kiesecker, J. M., Chivers, D. P., Marco, A. et al. 1999. Identification of a disturbance signal in larval red-legged frogs, *Rana aurora*. – *Anim. Behav.* 57: 1295–1300.
- Laurila, A., Kujasalo, J. and Ranta, E. 1998. Predator-induced changes in life history in two anuran tadpoles: effects of predator diet. – *Oikos* 83: 307–317.
- Levri, E. P. 1998. Perceived predation risk, parasitism, and the foraging behavior of a freshwater snail (*Potamopyrgus antipodarum*). – *Can. J. Zool.* 76: 1878–1884.
- Lima, S. L. 1990. The influence of models on the interpretation of vigilance. – In: Bekoff, M. and Jamieson, D. (eds), *Interpretation and explanation in the study of animal behaviour*. Vol. 2. Explanation, evolution and adaptation. Westview Press, pp. 246–267.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. – *Stress and Behav.* 27: 215–290.
- Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – *Can. J. Zool.* 68: 619–640.
- Loose, C. J., Vonefert, E. and Dawidowicz, P. 1993. Chemically-induced vertical migration in daphnia – a bioassay for kairomones exuded by fish. – *Arch. Hydrobiol.* 126: 329–337.
- Luttbegg, B. and Schmitz, O. J. 2000. Predator and prey models with flexible individual behavior and imperfect information. – *Am. Nat.* 155: 669–683.
- Madison, D. M., Maerz, J. C. and McDarby, J. H. 1999. Optimization of predator avoidance by salamanders using chemical cues: diet and diel effects. – *Ethology* 105: 1073–1086.
- McIntosh, A. R. and Townsend, C. R. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish induced changes to grazer behaviour? – *Oecologia* 108: 174–181.
- McNamara, J. M. and Houston, A. I. 1992. Evolutionarily stable levels of vigilance as a function of group size. – *Anim. Behav.* 43: 641–658.
- Murray, D. L. and Jenkins, C. L. 1999. Perceived predation risk as a function of predatory dietary cues in terrestrial salamanders. – *Anim. Behav.* 57: 33–39.
- Ojanguren, A. F. and Brana, F. 1999. Discrimination against water containing unrelated conspecific and a marginal effect of relatedness on spacing behavior in juvenile brown trout. – *Ethology* 105: 937–948.
- Peacor, S. D. and Werner, E. E. 1997. Trait-mediated indirect interactions in a simple aquatic food web. – *Ecology* 78: 1146–1156.

- Peckarsky, B. L. and McIntosh, A. R. 1998. Fitness and community consequences of avoiding multiple predators. – *Oecologia* 113: 565–576.
- Persons, M. H., Walker, S. E., Rypstra, A. L. and Marshall, S. D. 2001. Wolf spider predator avoidance tactics and survival in the presence of diet-associated predator cues (Araneae: Lycosidae). – *Anim. Behav.* 61: 43–51.
- Pulliam, H. R. 1973. Advantages of flocking. – *J. Theoret. Biol.* 38: 419–422.
- Relyea, R. A. 2000. Trait-mediated indirect effects in larval anurans: reversing competition with the threat of predation. – *Ecology* 81: 2278–2289.
- Relyea, R. A. 2002. Competitor-induced plasticity in tadpoles: consequences, cues, and connections to predator-induced plasticity. – *Ecology*, in press.
- Roberts, G. 1996. Why individual vigilance declines as group size increases. – *Anim. Behav.* 51: 1077–1086.
- Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. – *Am. Nat.* 151: 327–342.
- Stearns, S. C. 1989. The evolutionary significance of phenotypic plasticity. – *BioScience* 39: 436–445.
- Tollrian, R. and Harvell, C. D., eds. 1999. *The ecology and evolution of inducible defenses*. – Princeton Univ. Press.
- Turner, A. M. 1997. Contrasting short-term and long-term effects of predation risk on consumer habitat use and resources. – *Behav. Ecol.* 8: 120–125.
- Turner, A. M. and Mittelbach, G. G. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. – *Ecology* 71: 2241–2254.
- Werner, E. E. and Anholt, B. R. 1993. Ecological consequences of the trade-off between growth and mortality-rates mediated by foraging activity. – *Am. Nat.* 142: 242–272.
- Werner, E. E. and Peacor, S. D. 2003. A review of trait-mediated indirect interactions in ecological communities. – *Ecology*, in press.
- West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. – *Annu. Rev. Ecol. Syst.* 20: 249–278.
- Wilson, D. J. and Lefcort, H. 1993. The effects of predator diet on the alarm response of red-legged frog, *Rana aurora*, tadpoles. – *Anim. Behav.* 46: 1017–1019.
- Yamada, S. B., Navarrete, S. A. and Needham, C. 1998. Predation induced changes in behavior and growth rate in three populations of the intertidal snail, *Littorina sitkana* (Philippi). – *J. Exp. Marine Biol. Ecol.* 220: 213–226.